

The Athericidae, a new family in the lower Brachycera (Diptera)

by

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SYNOPSIS

Structural features of the male and female genitalia, abdominal base, thorax, wing venation and antennae, as well as larval morphology, indicate that the following genera formerly included in the Rhagionidae, viz. *Atherix* Meigen, *Atrichops* Verrall, *Suragina* Walker, *Pachybates* Bezzi, *Trichacantha* Stuckenberg, *Dasyomma* Macquart and *Xeritha* Stuckenberg, form a monophyletic group whose sister-group is not the genus *Rhagio* Fabr. and its relatives but the Tabanidae. The new family Athericidae, type-genus *Atherix*, is erected for these genera. The relationship between tabanids and athericids is apparent in oviposition and haematophagous habits common to both families. A new subfamily, Dasyomminae, is erected for *Dasyomma* because the genus has many morphological distinctions. The sister-group of the Rhagionidae is considered to be the Coenomyiidae, and both Rhagionidae and Pelecorhynchidae are rejected as members of the Tabanoidea *sensu* Hennig.

INTRODUCTION

The so-called 'lower Brachycera', namely the relatively primitive eremochaetous brachycerous flies with a pulvilliform empodium, comprise an interesting and attractive sector of the Diptera that has drawn the attention of some of the best students of the order. There have been many attempts to find a generally acceptable classification of these flies at suprageneric levels, accounts of which may be obtained from publications such as those of Verrall (1909), Pleske (1925), Steyskal (1953) and Hennig (1954, 1967), but despite this not inconsiderable amount of attention, the taxonomy remains unsatisfactory and unsettled.

The following arrangement of families published by Hennig (1967) represents a portion of present-day opinion; in his scheme three superfamilies are recognized:

<i>Xylophagoidea</i>	<i>Stratiomyioidea</i>	<i>Tabanoidea</i>
Coenomyiidae	Xylomyidae	Rhagionidae
Pantophthalmidae	(= Solvidae)	Pelecorhynchidae
(= Acanthomeridae)	Stratiomyiidae	Tabanidae
Rachiceridae		
Xylophagidae		
(= Erinnidae)		

The limits of many of the families listed above has been a contentious matter, and probably only the delimitation of the Pantophthalmidae has not been controversial. The other families within Hennig's Xylophagoidea and Stratiomyioidea have been variously fragmented and combined with one another, and in the Tabanoidea the status of the Pelecorhynchidae has been considered by some authors to be doubtful as a result of the conclusive finding of Mackerras & Fuller (1942) that *Pelecorhynchus* Macquart cannot be included in the Tabanidae. In some older classifications, such as that of Leonard (1930), the Rhagionidae included the Xylomyidae, Rachiceridae, Coenomyiidae and Xylophagidae of Hennig. In general,

the main problems have been the delimitation of monophyletic suprageneric groups, the rank these groups should have, and the desirability and constitution of superfamilies.

The central group in this complex taxonomic history has been the Rhagionidae as this family contains, by common consent, a core of genera whose affinities appear to extend in all directions to the other groups of lower Brachycera, no matter how constituted. A relationship with the Tabanidae has been indicated by a number of authors, notably Bezzi (1903), Hennig (1967), Mackerras & Fuller (1942), Pleske (1925), Roskošný & Spitzer (1965), and Verrall (1909), and most authors have noted or expressed in their classifications affinities between the Rhagionidae, Xylophagidae and Xylomyidae. The extent to which these groups have been divided up and merged with the Rhagionidae has varied according to the characters selected by authors for defining the Rhagionidae, and much of the uncertainty and debate about the classification has been due to the use of grade characters such as the degree of compaction of the antennal flagellum and the number of tibial spurs and various combinations in which they occur on the various pairs of legs.

Throughout the tangled taxonomic history of the lower Brachycera, one of the few invariable features has been the inclusion of the genus *Atherix* Meigen in the Rhagionidae, along with obviously related genera such as *Suragina* Walker and *Atrichops* Verrall which have sometimes been considered to be synonyms. All classifications of the Rhagionidae that have been proposed or used include *Atherix* without question: examples are Becker (1922), Bezzi (1903, 1912, 1926), Brunetti (1909, 1920), Frey (1954), James (1965, 1968), Kertész (1908), Krizelj (1971), Leonard (1930), Lindner (1925), Lundbeck (1907), Malloch (1917), Paramonov (1962), Pleske (1925), Rondani (1856), Roskošný & Spitzer (1965), Séguy (1926), Steyskal (1953), Szilády (1934), Verrall (1909) and Wahlgren (1907). Furthermore, *Atherix* usually is placed next or close to *Rhagio* Fabr., a close relationship thereby being implied, or in the same subfamily, the Rhagioninae. Nearly all these classifications use the same set of characters, and if the authors give keys, the keys are structured in a singularly constant way. Typically, a key to rhagionid genera will segregate *Rhagio* and *Atherix* from the other genera by means of the tibial spur formula; *Atherix* then will be distinguished by its reniform third antennal segment from *Rhagio* which has an oval or a round or conical third segment. This strategy has a long history and has been copied over and over again; apparently because of its simplicity, the ease with which it can be applied, and its regular use by authoritative and charismatic Dipterists, it has effectively diverted attention from the existence of many profound differences between these two genera in their morphology and biology. I know of only one paper, that by Malloch (1932), in which some previously ignored differences between *Rhagio* and *Atherix* have been pointed out.

It is the purpose of the present study to show that this long-accepted classification is not tenable because *Atherix* and its relatives in fact have no close affinity with *Rhagio* and indeed cannot even be retained in the same family.

COMPARATIVE MORPHOLOGY

For the sake of brevity and the avoidance of repetition, I shall refer to the genera *Atherix* Meigen, *Atrichops* Verrall, *Dasyomma* Macquart, *Pachybates* Bezzi, *Suragina* Walker, *Trichacantha* Stuckenberg and *Xeritha* Stuckenberg, collectively as the athericiform genera. The following will be referred to as the rhagioniform genera: *Rhagio* Fabricius,

Chrysopilus Macquart, *Symphoromyia* Frauenfeld, *Dialysis* Walker, *Ptiolina* Zetterstedt, *Arthroceras* Williston, *Atherimorpha* White, *Arthroteles* Bezzi, *Spania* Meigen and *Spaniopsis** White. I have not been able to study *Omphalophora* Becker, *Schizella* Bezzi, *Rhagina* Malloch and *Stylospania* Frey, but it seems likely that they are members of the rhagioniform group. The genera *Austroleptis* Hardy, *Bolbomyia* Loew, *Lampromyia* Macquart, *Vermileo* Macquart, *Vermitigris* Edwards and *Pelecorhyncus* Macquart, as well as most of the genera that are generally accepted as Coenomyiidae, have also been examined; their relationships with the rhagioniform genera are still undetermined or uncertain, and they are excluded from this study.

In this section I shall give an account of certain morphological fields in which the athericiform genera differ from the rhagioniform genera and resemble the Tabanidae. The fields discussed have been selected because they provide clear evidence of relationships and give insight into evolutionary trends within the groups. No claim to comprehensiveness in this selection is made or implied. Additional aspects of adult morphology could have been included, but it is considered that the data provided below are adequate for establishing monophyletic groups and determining sister-group relationships.

1. *The male genitalia*

For the purposes of this paper I am adopting the morphological terminology used by Bonhag (1951) for Tabanidae; it is necessary to point out that what he calls the 'endophallic apodeme' (ea) is usually known as the aedeagal apodeme, a term he confusingly applies to the two struts (aa) projecting cephalad from the upper surface of the hypopygium.

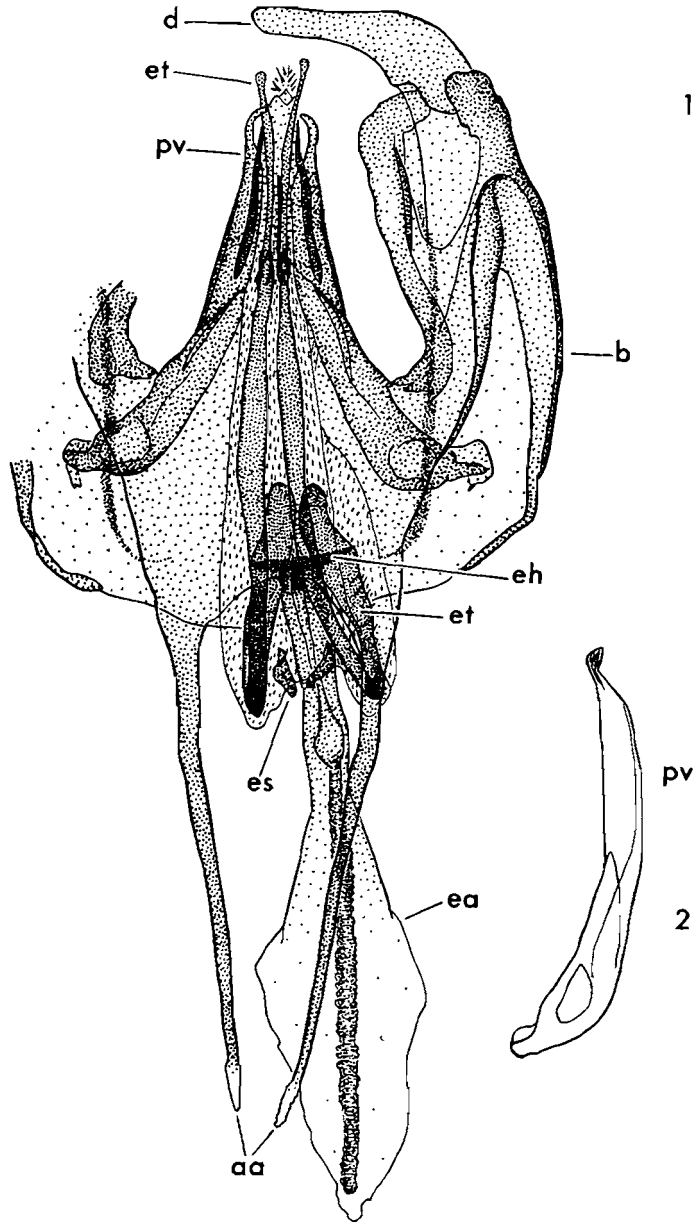
In the athericiform genera the hypopygium is of constant basic construction and is characterized by the features described below. See figs 1-4, 11, 12; published illustrations, varying in accuracy and completeness, are available as follows: *Atherix*, Nagatomi (1958: fig. 17), Roskošný & Spitzer (1965: figs 33-37, 40, 41); *Atrichops*, Nagatomi (1958: figs 20, 21, as *Heterosuragina*), Roskošný & Spitzer (1965: figs 38, 39); *Suragina*, Nagatomi (1958: figs 18, 19); *Pachybates*, Stuckenberg (1960: figs 70, 71, 74, 75); *Trichacantha*, Stuckenberg (1960: figs 79, 80); *Xeritha*, Stuckenberg (1966: figs 6, 7).

(a) The ninth sternite is completely fused with the basistyles.

(b) There is no definite, sclerotized bridge joining the upper edges of the two basistyles over the dorsal part of the aedeagal base.

(c) The aedeagus contains a pair of curved, sclerotized rods, called 'endophallic tines' by Bonhag (1951: 161), and, unsuitably, 'flagella' by Mackerras (1954: 444-445, and other papers) and Stuckenberg (1966: 59, and other papers). These tines (et) are attached on each side of the endophallic apodeme (ea) near its apex, at a point where there is a sclerotic thickening called the endophallic hilt (eh), and each tine has there a dilated terminal part bearing microscopic setae. At their base these tines are directed cephalad, but they soon curve right over to extend caudad right to the apex of the aedeagus from which they often protrude in preparations.

* Paramonov (1962) made *Spaniopsis* a synonym of the palaearctic *Spania*, but gave no reason for doing so; pending clarification, the synonymy is not accepted here.



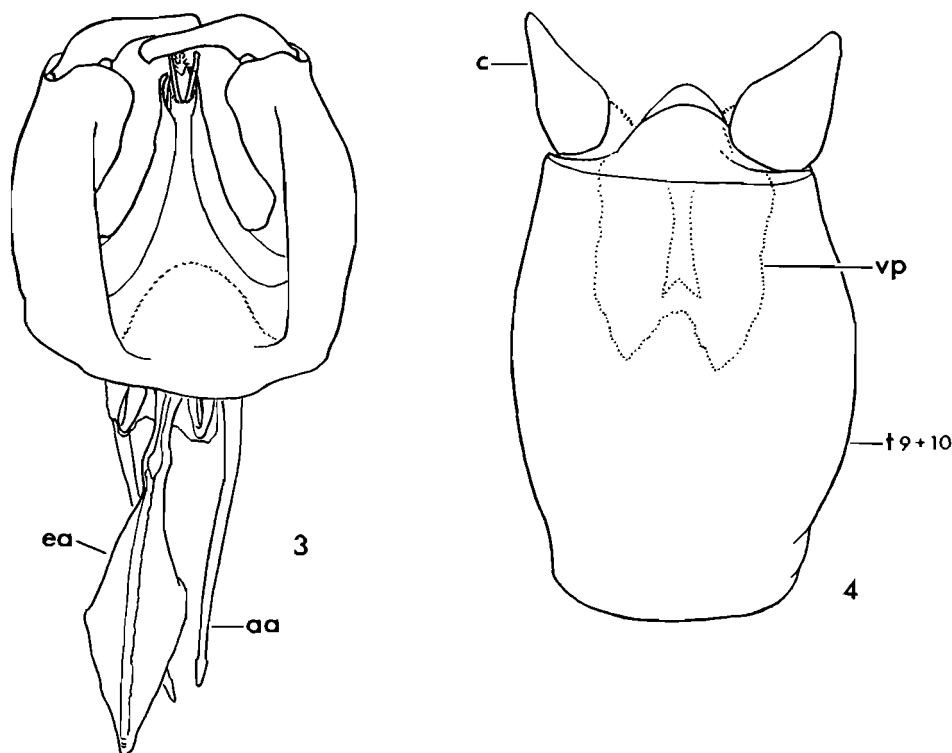
Figs 1-2. *Suragina monogramma* (Bezzi). (1) Hypopygium, dorsal view; (2) penis valve, lateral view. Lettering: aa = aedeagal apodeme; b = basistyle; d = dististyle; ea = endophallic apodeme; eh = endophallic hilt; es = endophallic supporting sclerite; et = endophallic tine; pv = penis valve.

(d) The upper surface of the aedeagus is extended cephalad and is produced into two long, slender aedeagal apodemes (aa) which reach far beyond the basal margin of the sternal area.

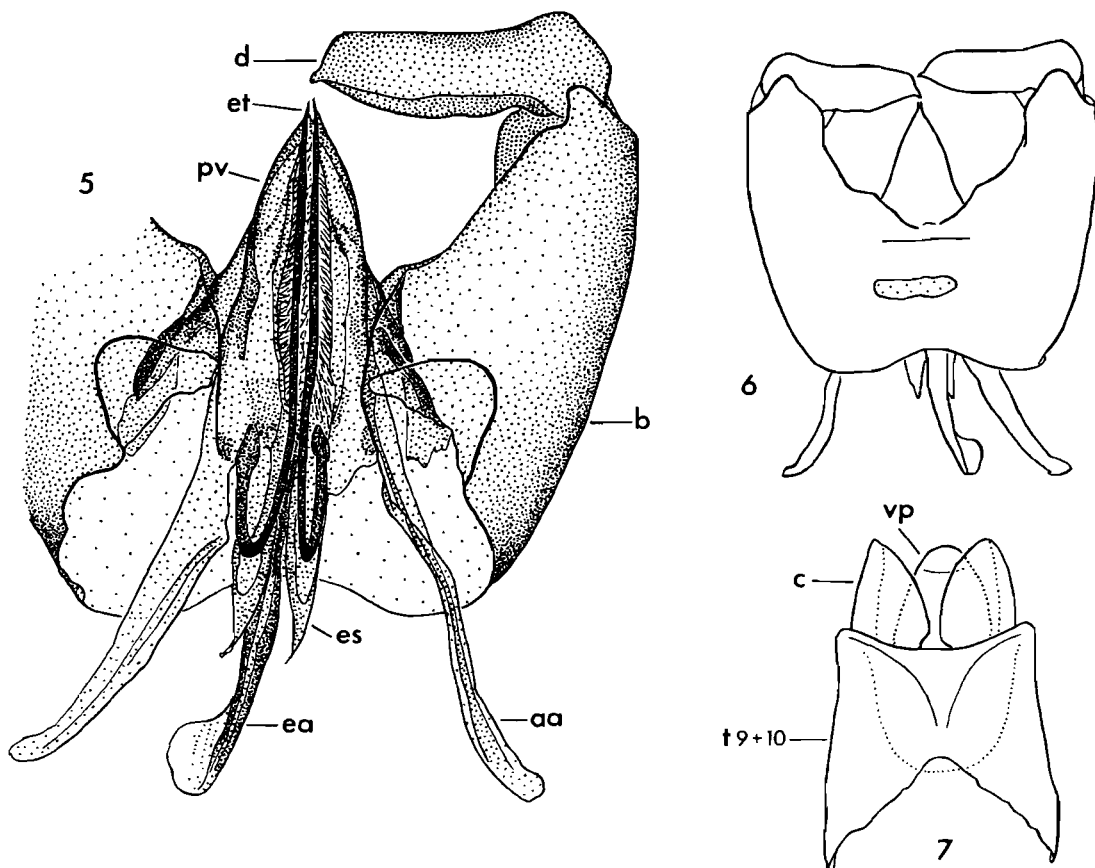
(e) The aedeagus is sheathed on each side by a sclerotized penis valve which in most genera has a curved apex (figs 1, 2, pv).

(f) The dorsal components of the hypopygium comprise only the epandrium and proctiger which together form a highly characteristic compound structure (fig. 4). The epandrium is longitudinally elongate to varying degrees and narrows posteriorly; the cerci are attached to its posterior edge where they are prominently visible, and they cannot be withdrawn, so only the ventral plate of the proctiger (vp) extends beneath the epandrium. This arrangement suggests that the epandrium is formed of fused tergites nine and ten, which is the interpretation given by Bonhag (1951) for Tabanidae.

In almost all these important, probably apomorphic features the athericiform genera agree with the Tabanidae; see figs 5-7, 13, and the many illustrations by Mackerras (1954, 1955, and subsequent papers) and Bonhag. The agreement extends also to many lesser morphological details. The only notable difference is not a fundamental one: tabanids are more apomorphic in that the epandrium is longitudinally divided in Chrysopsinae and Tabaninae, and basally emarginate in Pangoniinae (fig. 7). Other differences are minor:



Figs 3-4. *Suragina monogramma* (Bezzi). (3) Hypopygium, ventral view; (4) epandrium, dorsal view. Lettering, see figs. 1-2, also: c = cercus; t = tergite, numbered to indicate abdominal segmentation; vp = ventral plate of proctiger.



Figs 5-7. *Philoliche (Phara) bicingulata* Oldroyd. Hypopygium in dorsal (5) and ventral (6) views; (7) epanandrium, dorsal view. Lettering as in preceding figures.

for example, I know of no tabanid having the apex of the penis valve curved, and the endophallic apodeme is sometimes produced far beyond the endophallic hilt (fig. 13).

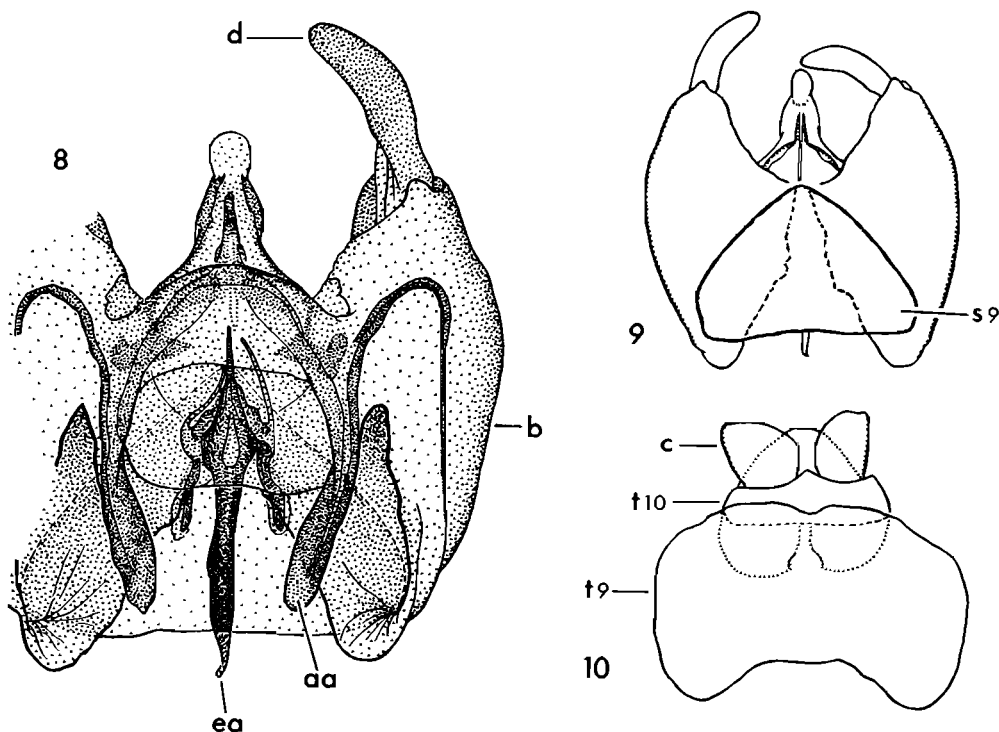
In the rhagioniform genera the hypopygium differs as follows (see figs 8-10; illustrations are available for *Rhagio*, *Chrysopilus*, *Symphoromyia* and *Spania* in Roskošný & Spitzer, 1965; for *Arthroteles*, see Stuckenberg, 1956):

(a) The hypandrium is not fused with the basistyles in a majority of the genera (*Rhagio*, *Arthroceras*, *Atherimorpha*, *Arthroteles* and *Ptiolina*). In *Symphoromyia* and some species of *Chrysopilus* it is fused basally but separated distally, and in *Spaniopsis* and other species of *Chrysopilus* it is completely fused. Fusion is the apomorphic state, but in other respects these genera do not appear to have a very close relationship, so convergence is assumed; the fused condition of the basistyles and hypandrium in the athericiform genera must have been independently attained.

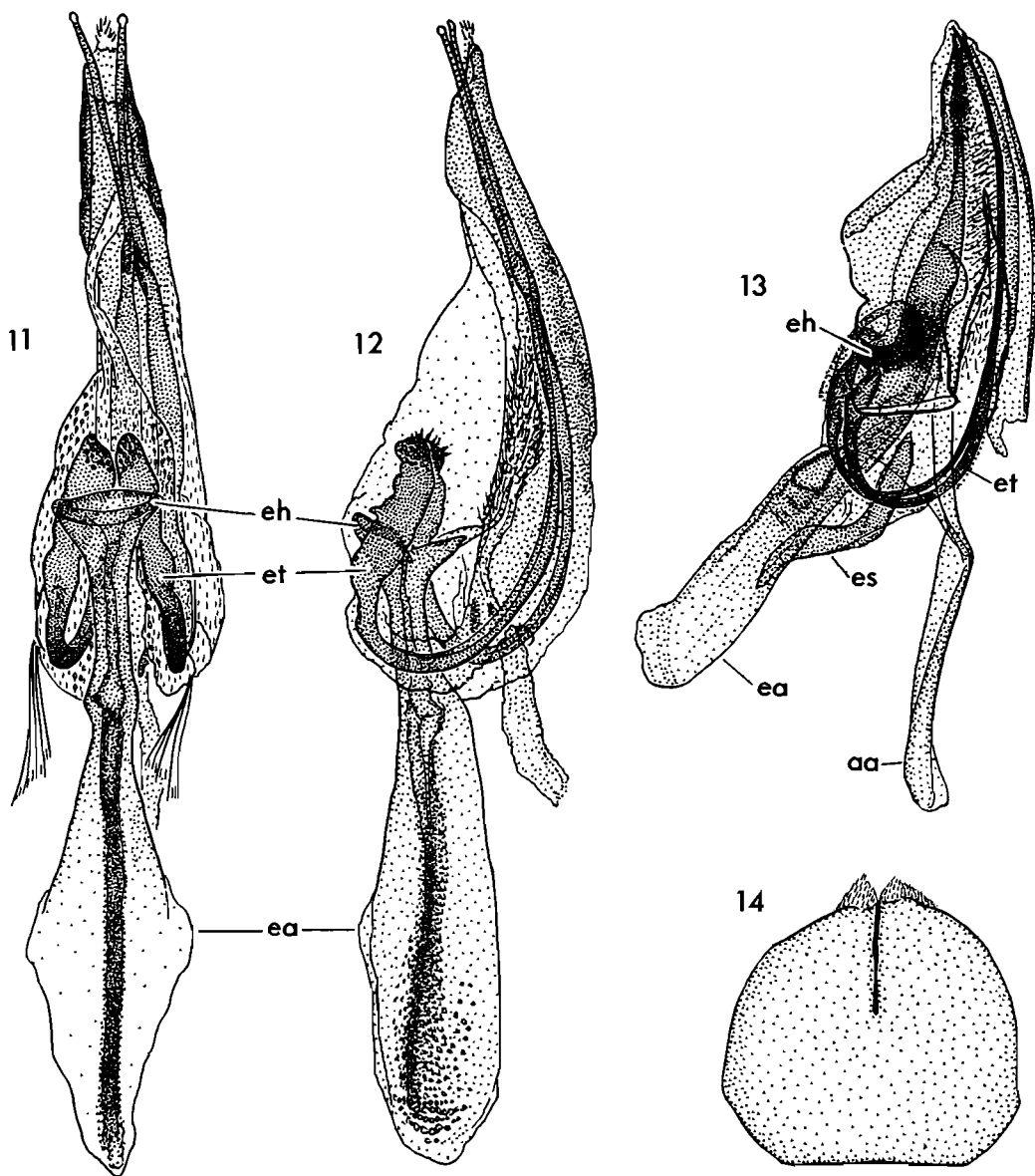
(b) There is usually a definite sclerotization that bridges the dorsal part of the aedeagus basally (fig. 8) between the inner margins of the basistyles.

(c) The aedeagus contains no endophallic tines like those characteristic of the other two groups, a difference at once apparent in preparations. What appear to be precursor conditions can however be demonstrated; careful study has shown that in some species (*Rhagio scolopacea*, fig. 8, and some South African and Australian species of *Atherimorpha*) there is a pair of very small, weak, curved rods that arise at a subapical swelling on the endophallic apodeme. These are situated at the same place at which the tines are attached, and have the same spatial relationship with the endophallic sclerites (es); however, their smallness and weakness, and relationship with other parts of the aedeagus, indicate that they cannot function in the same way as the tines. In *Chrysopilus* species there is a pair of minute, microsetose sclerites immediately posterior to the distal end of the endophallic apodeme; these appear to be comparable in their sensory nature and position to the microsetose apex of the endophallic tines, adjacent to the endophallic hilt in the athericiform genera and tabanids.

(d) An aedeagal apodeme (fig. 8, aa) projects from the upper, inner edge of the basistyle



Figs 8-10. *Rhagio scolopacea* (Linn.). Hypopygium in dorsal (8) and ventral (9) views; (10) epandrium, dorsal view. Lettering as in preceding figures, also: s = sternite, numbered to indicate abdominal segmentation.



Figs. 11-14. (10, 11) *Suragina monogramma* (Bezzi), aedeagus in ventral and lateral views; (13) *Philoliche (Phara) bicingulata* Oldroyd, aedeagus in lateral view; (14) *Suragina bezzii* (Curran), female hypogynium or eighth sternite. Lettering as in fig. 1.

cephalad, but it is relatively much shorter, not passing cephalad beyond the ventral basal margin of the hypopygium.

(e) The aedeagus comprises essentially a basal sac, often of subhemispherical form, from which arises a tube of variable form; there is no development of penis valves comparable to those of tabanids or the athericiform genera.

(f) The epandrium typically is transverse, and the tenth tergite (when present) and cerci are withdrawn to varying degrees beneath it; other arrangements are few and represent unusual modifications in which the whole hypopygium assumes a different posture (as in *Symphoromyia*). The identity of the epandrium as only the ninth tergite is in no doubt because a morphological series is present in which, at one extreme, the tenth tergite is represented as a transverse entity, either sclerotized or semi-membranous (fig. 10), or is divided in the midline into two lateral portions which show various degrees of reduction (both states are found in *Chrysopilus*). At the other extreme, namely those cases in which no trace of a tenth tergite can be found (e.g. *Arthroteles*), apparently median splitting has been succeeded by loss through reduction, probably to facilitate retraction of the proctiger.

2. The female genitalia

The female abdomen in the athericiform genera has the following features (see figs 14–20):

(a) The apical part of the abdomen is relatively flattened dorsoventrally and the side margins of the tergites project laterally; this is especially noticeable in members of the large genus *Suragina*, in *Atrichops* and in the South African genera.

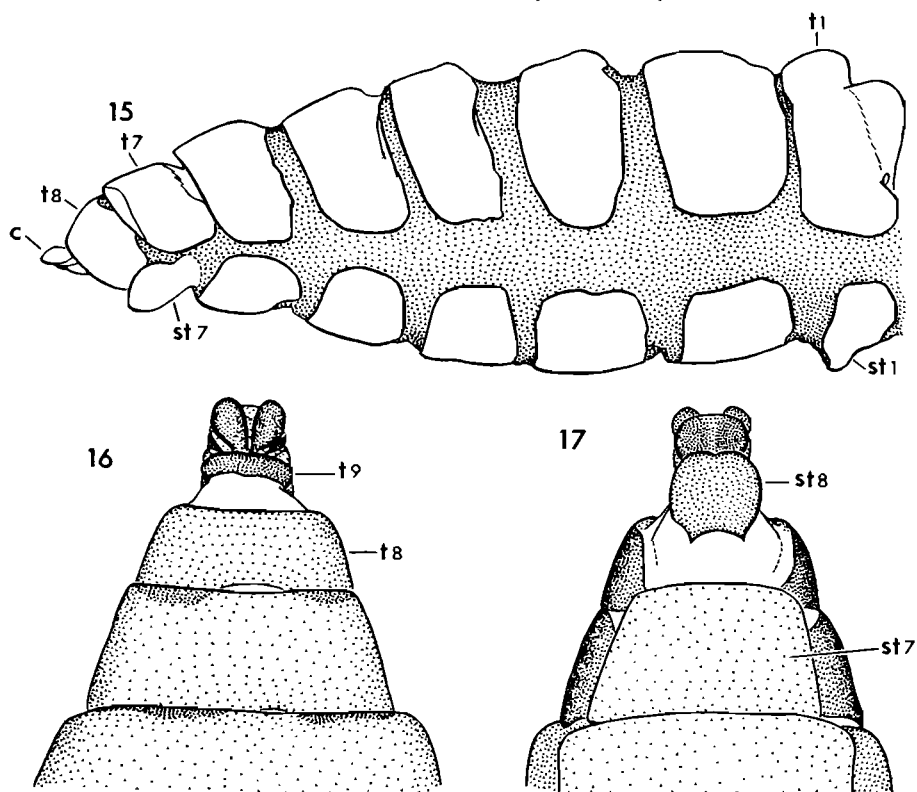
(b) The tergites and sternites are only narrowly separated when the abdomen is fully extended (fig. 15), due to the relatively small area of the pleural and intersegmental membranes, and there is no strong telescoping of segments.

(c) Eight tergites are always exposed, though the eighth usually is partly withdrawn beneath the seventh. The postabdomen essentially is confined to the genital and postgenital segments and in repose is retracted beneath the eighth tergite (fig. 15).

(d) The postabdomen (figs 18–20) is a discrete, compact structure separated by expanses of membrane from the eighth tergite and seventh sternite (figs 16, 17). It comprises dorsally a simple, reduced, transverse ninth tergite, and a divided tenth tergite represented by two narrow, separated, sometimes inwardly tapering sclerites which always are inclined cephalad at the inner end; succeeding the tenth tergite is a pair of simple, undivided cerci. Ventrally there is a roughly cordate or obcordate hypogynium (fig. 14) and the ventral plate of the proctiger. An irregular lateral area of sclerotization is variably developed on each side of the ninth tergite (fig. 20).

The female abdomen in the rhagioniform genera is very different and extremely constant in structure (see figs 21–24):

(a) The abdomen, including the terminal part, is generally cylindrical, and the segments decrease regularly in diameter so that the abdomen tapers strongly.



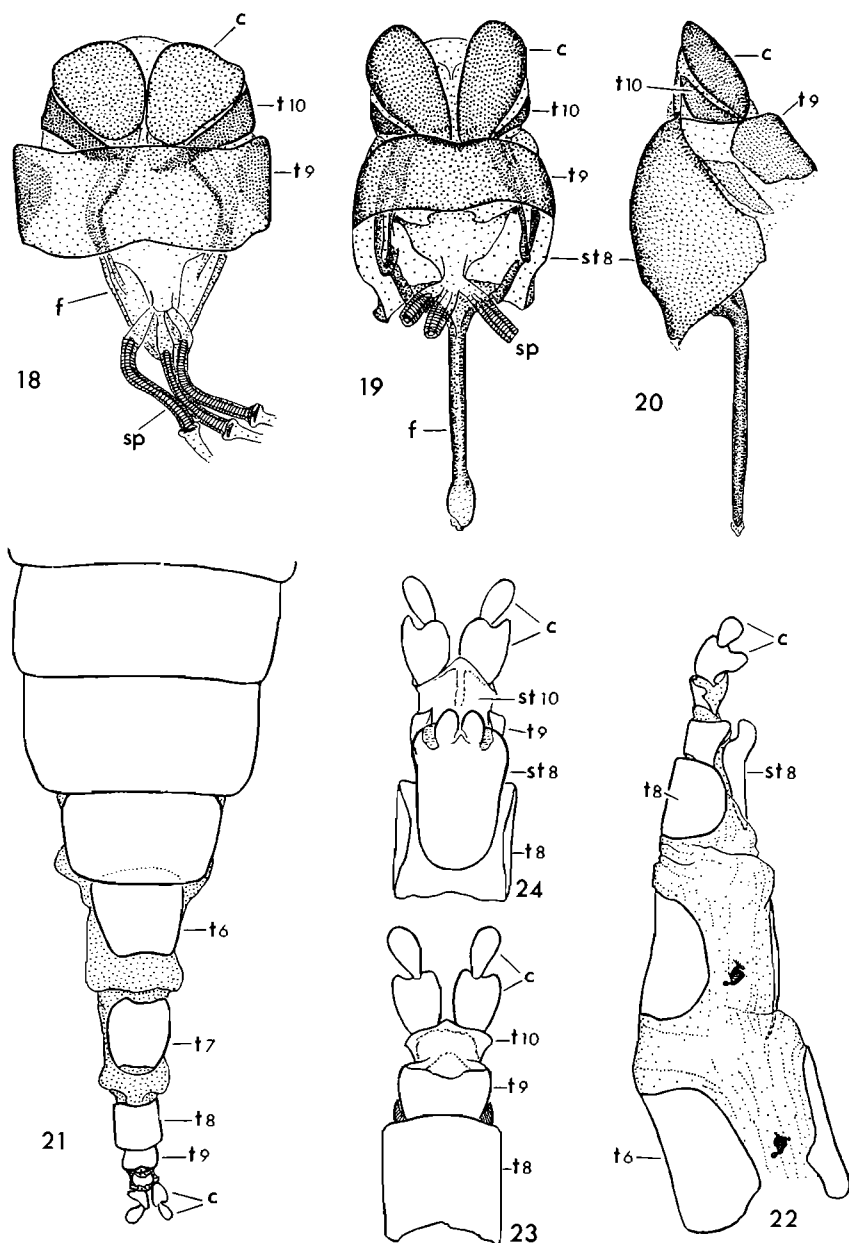
Figs 15-17. *Atherix ibis* Fabr. female. (15) Entire abdomen in lateral view, extended except for genitalia; (16, 17) apical part of abdomen with genitalia extended, in dorsal and ventral views. Lettering: c = cercus; t = tergite, st = sternite, numbered to indicate abdominal segmentation.

(b) The pleural membranes usually are extensive, and there are wide intersegmental membranes, especially beyond the sixth segment; a marked telescoping of segments is characteristic, so that when the entire abdomen is extended, it is greatly increased in length (probably an adaptation for terrestrial oviposition). *Spaniopsis* is an exception in that these membranes are relatively smaller and the whole abdomen is more compact, possibly an adaptation for blood-sucking habits.

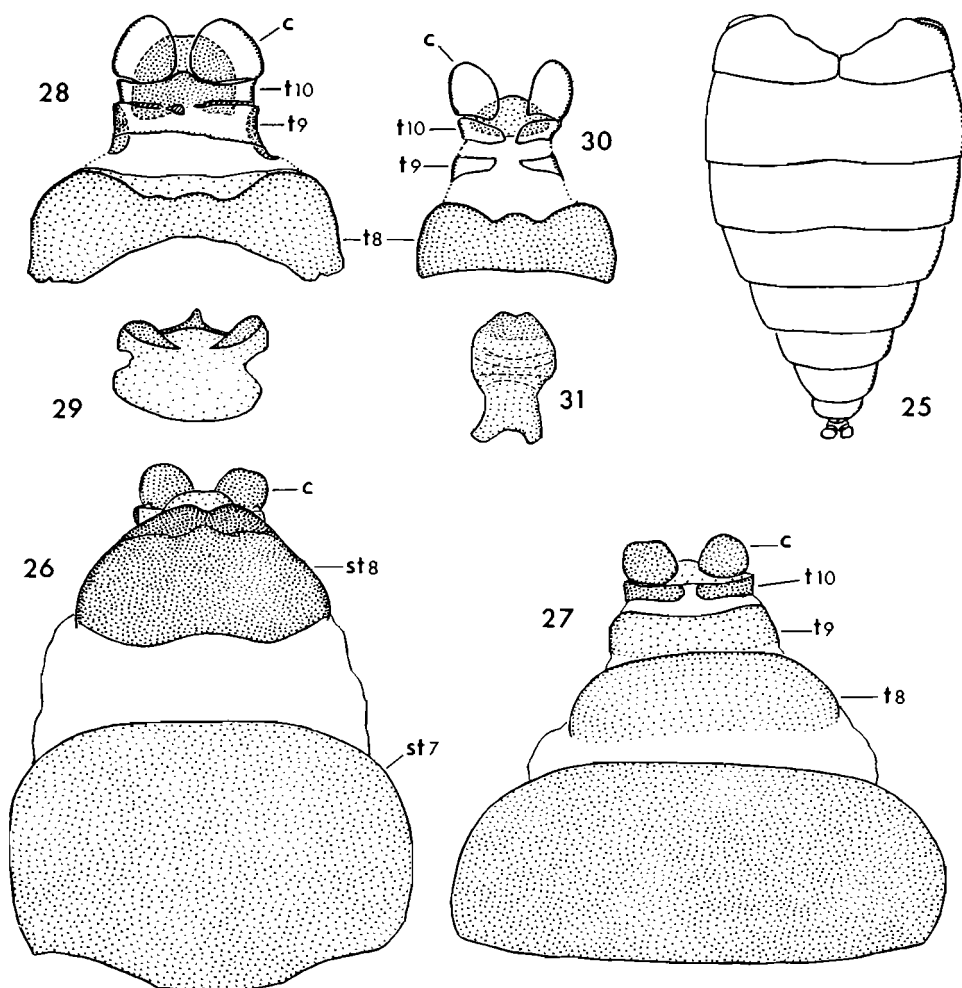
(c) There is no clearly demarcated postabdomen, though the decrease in diameter is obvious after about the fifth segment, and the segments after the sixth are much telescoped.

(d) The eighth tergite, a simple, reduced, arched plate, is widely separated from the seventh but only narrowly separated from the ninth tergite; the tenth tergite is represented by a variably sclerotized area bounded by membrane, and is followed by the highly characteristic cerci which are clearly two-segmented. The hypogynium shown in fig. 24 is representative.

In Tabanidae (figs 25-31; see the many figures given by Mackerras, 1954, 1955, and subsequent papers, and by Bonhag, 1951, and Bromley, 1926):



Figs 18-24. Female abdominal structures. (18) *Suragina bezzii* (Curran), genital segments and proctiger, dorsal view. (19, 20) *Atherix ibis* Fabr., genital segments and proctiger, dorsal and lateral views. (21-24) *Rhagio scolopacea* (Linn.); (21) apical portion of abdomen, dorsal view; (22) postabdomen, lateral view; (23, 24) genital segments and proctiger, dorsal and ventral views. Lettering, as in preceding figures, also: f = female genital furca; sp = spermatheca.



Figs 25-31. Female abdominal structures. (25) *Tabanus taeniola* P. de B., entire abdomen, dorsal view. (26, 27) *Ectenopsis angusta* (Macq.), postabdomen in ventral and dorsal views. (28, 29) *Philoliche* (*Phara*) *bivirgulata* (Austen); (28) epigynum and proctiger, dorsal view; (29) hypogynium, ventral view. (30, 31) *Tabanus saxicolus* Usher; (30) epigynum and proctiger, dorsal view; (31) hypogynium, ventral view.

- (a) The abdomen is dorsoventrally flattened progressively apicad, and the side margins of the tergites often project laterally as in the athericiform genera.
- (b) Intersegmental and pleural membranes in general are narrow, and there is hardly any telescoping of segments, even in species with a strong reduction towards the apex of the abdomen in the size of the tergites and sternites (fig. 25).
- (c) Seven tergites are exposed, at least in dried specimens. The postabdomen, as in the athericiform genera, is a discrete, clearly-defined structure comprising the eighth tergite and genital and postgenital segments (figs 26, 27). The eighth tergite is invariably reduced and usually specialized in that it is medially constricted or excised.
- (d) The postgenital segments are represented, dorsally, by small, strongly transverse ninth and tenth tergites; the tenth is split in the midline in all tabanids except a few Pangoniini (Philip & Coscarón, 1971) and Philolichini (fig. 28); the ninth tergite is undivided in Pangoniinae (fig. 28) but divided in Chrysopsinae and Tabaninae (fig. 30). The cerci are simple and undivided. The hypogynium is of varied form (e.g. figs 29, 31) and is sometimes useful taxonomically at the subfamily level (Mackerras, 1954).

The many resemblances between the athericiform genera and the Tabanidae are obvious, and include the rigidity, slight extensibility and apical flattening of the abdomen, the discreteness and compaction of the postabdomen, the reduction of the ninth and tenth tergites to narrow, transverse bands, the medial division of the tenth tergite, and (but this may be a plesiomorphic character) the simple, one-segmented cerci. The Tabanidae are more apomorphous in that the eighth tergite is modified, and in two subfamilies also the ninth tergite is divided.

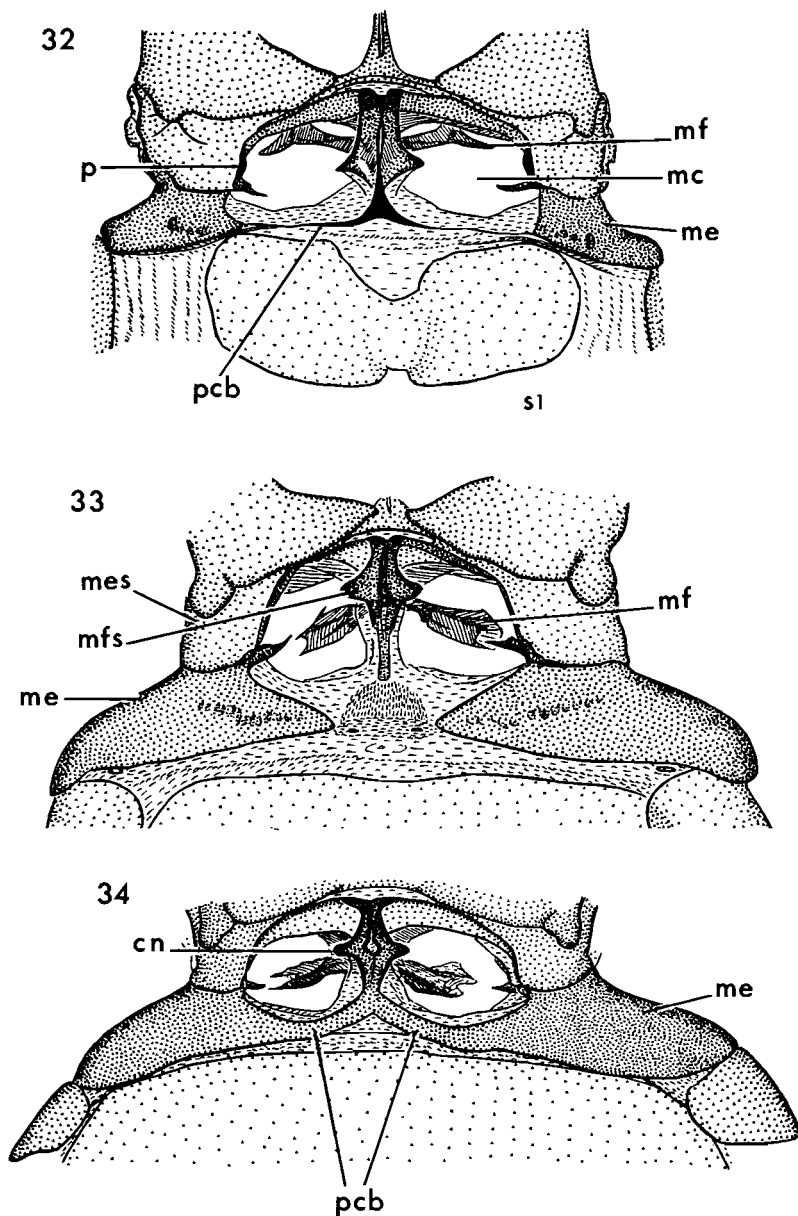
3. Structure of the base of the abdomen

The athericiform genera are distinguished by the following feature:

- (a) In the postmetacoxal membrane—i.e. the membrane connecting the abdomen to the thorax ventrally—there is a slender but definite sclerotic strip on each side (see figs 32, 35), that commences as a continuation of the lower end of the metapleural epimeron (me) and runs to the ventral midline; in the midline the two strips unite and connect with the posterior end of the metafurcasternum (mfs) which is prolonged caudad, thus closing off each of the hind coxae posteriorly. Figure 32 shows *Atherix ibis* (Fabr.) which has this feature in a relatively plesiomorphic state; the postmetacoxal bridge (pcb) is weak and thin, and best seen after staining except for the inverted-Y-shaped connection to the metafurcasternum. Figure 35 shows *Suragina monogramma* (Bezzi) in which the postmetacoxal bridge is well-developed and typical of the more apomorphous members of this group of genera.

In addition, these genera have the following features as well:

- (b) There is a conspicuous trend towards a median division of the first tergite by a longitudinal suture; this feature is part of a suite of apomorphous developments whose most advanced expression is in the blood-sucking and tropical members of the group, especially the large genus *Suragina*. It may be a sexual feature (commonly in females only), or found only in some species in a genus, or absent in all species of a genus (only small or monotypic genera).



Figs 32-34. Ventral view of area of attachment of thorax and abdomen. (32) *Atherix ibis* Fabr., female; (33) *Tabanus saxicolus* Usher, male; (34) *Philoliche (Phara) bivirgulata* (Austen), female. Lettering: cn = condyle; mc = metacoxal cavity; me = metapleural epimeron; mes = metapleural episternum; mf = metasternal furca; mfs = metafurcasternum; pcb = postmetacoxal bridge. All specimens slightly flattened; fig. 32 from specimen lightly stained with acid fuchsin.

(c) The postscutellum is developed as a curving, rounded ridge (see Malloch, 1932).

In the Tabanidae all species have the first tergite divided in the midline by a longitudinal suture, and a postmetacoxal bridge is always developed as a result of extension of the metapleural epimera behind the metacoxae. These two characters are excellent for diagnostic purposes but appear to have been overlooked hitherto. In Tabaninae (fig. 33) and Chrysopsinae, it is generally the case that the metapleural epimera do not meet ventrally, but are separated by a strengthened area in the ventral membrane, to which the metafurcasternum (mfs) is connected by a linear extension. In some Pangoniinae there is a much stronger strip of membrane bridging the gap between the ends of the epimera, but in others the epimera are connected to one another and to the metafurcasternum (fig. 34, me, pcb), the postmetacoxal bridge thus being complete. All Tabanidae have the postscutellum formed as it is in the athericiform genera.

The metafurcasternum in both the Tabanidae and the athericiform genera has a well-developed condyle on each side (see fig. 34, cn), on which the metacoxa articulates (see fig. 35).

In the rhagioniform genera:

(a) The metapleural epimera end below at the upper posterior corner of the metacoxae; the usual membrane, of variable extent, lies between the metacoxae and the first sternite, but there is no trace of sclerotic strips like those in the athericiform genera, and never postmetacoxal bridges formed by the epimera.

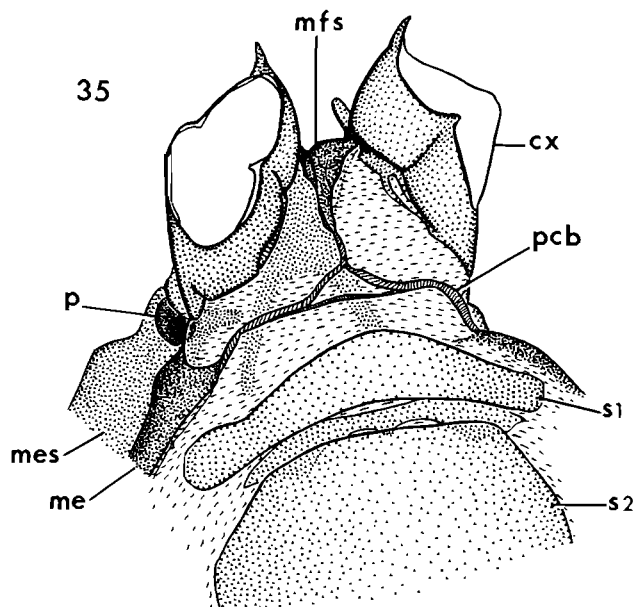
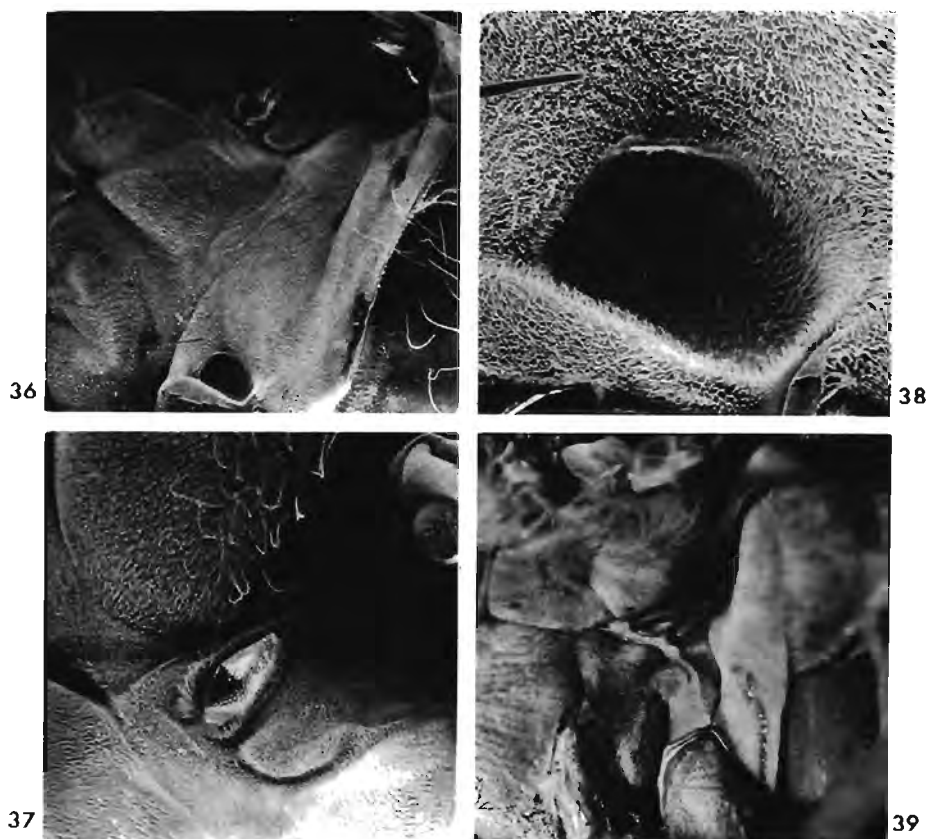


Fig. 35. *Suragina monogramma* (Bezzi), male; posterior-oblique of area of attachment between thorax and abdomen. Lettering as in preceding figures, also: cx = metacoxa; p = suprametacoxal pit; s = sternite.



Figs 36-39. Thoracic structures. (36-38) *Suragina monogramma* (Bezzi); (36) lateral view of posterior part of thorax, showing at upper middle the metathoracic spiracle and 'scale' immediately behind it, and at lower middle the suprametacoxal pit characteristic of the subfamily Athericinae; (37) enlarged view of metathoracic spiracle and 'scale'; (38) enlarged view of suprametacoxal pit. (39) *Tabanus par* Walker, lateral view of posterior parts of thorax and base of abdomen, showing at centre the metathoracic spiracle and prominent 'scale' immediately behind it. Figs 36-38 taken with scanning electron microscope, fig. 39 with light microscope.

(b) The first tergite is not divided medially, except in the Australian genus *Spaniopsis* (some of whose species are blood-suckers!); this tergite may thus also be divided in the palaearctic genus *Spania*, but I cannot determine this from my poor material of that genus.

(c) The postscutellum is of a different form, in most genera being obviously more flattened and not markedly curved (see Malloch, 1932).

A cursory study of the metacoxae of *Rhagio* reveals that they differ from those of the groups being compared in being relatively elongate and in having semi-membranous inner and posterior walls; the metafurcasternum is not extended posteriorly and has no well-formed condyles but instead a weak sclerotic connection to the coxa. Much remains to be investigated as regards the nature of the coxae in the lower Brachycera.

4. *The postmetaspiracular 'scale'*

Oldroyd (1952:4) has drawn attention to the presence of a small but distinct scale-like elevation in the strong membrane immediately posterior to the metathoracic spiracle of Tabanidae. This appears to be present in all members of the family (H. Oldroyd, I. M. Mackerras, *in litt.*), and is variably developed; in the Pangoniinae it is often relatively flat, whereas in the Chrysopsinae and especially the Tabaninae (fig. 39) it is more elevated and elongate, and strongly emphasized by the depth of the delimiting fold. In the athericiform genera the same scale-like structure is present in the membrane behind the metathoracic spiracle (figs 36, 37); in all the genera it is rather flat and more or less resembles the condition, probably relatively plesiomorphic, of this structure in various Pangoniinae. In the rhagioniform genera there is no such differentiation of the postmetaspiracular membrane.

5. *Wing venation*

In the athericiform genera (see figs 40, 43–45) the wing venation has one character that is virtually diagnostic for the group as a whole, and also many subtle features which collectively can be used to distinguish this group of genera from the rhagioniform genera (figs 42, 46, 47). With practice, the venation can be used to distinguish these two groups at a glance, even if the first of the following characters is ignored.

(a) In the athericiform genera the marginal cell is closed or very nearly closed by R_{2+3} meeting the costa at the end of R_1 . The only rhagioniform flies I know to have this feature are some species of *Chrysopilus*. In the Tabanidae (fig. 41) the marginal cell is always open.

(b) The fork of R_4 and R_5 is at a more acute angle; whereas in the rhagioniform genera this angle is usually much less acute and may even be almost a right-angle. In Tabanidae the venation is apomorphously modified by elongation of the apical part of the wing which has extended the marginal cell and resulted in the wide fork of R_4 and R_5 .

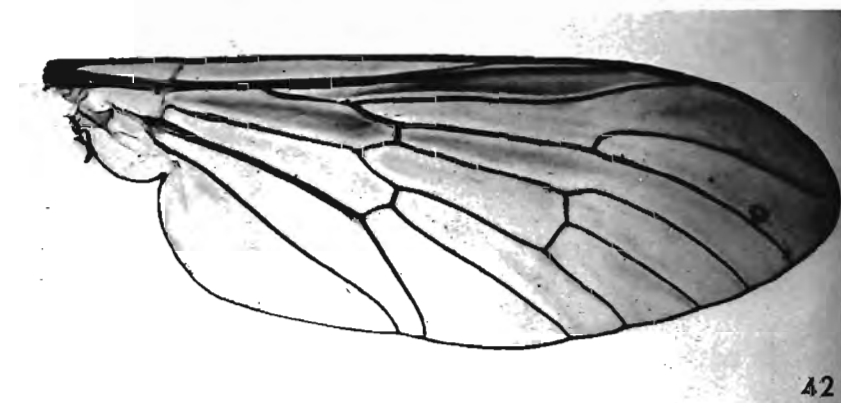
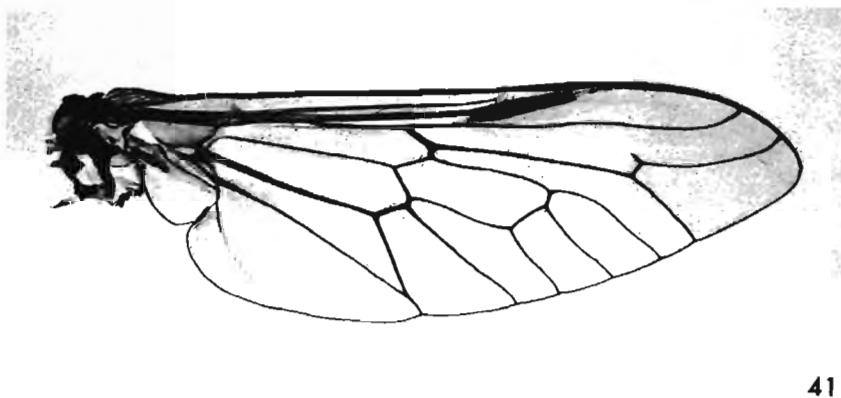
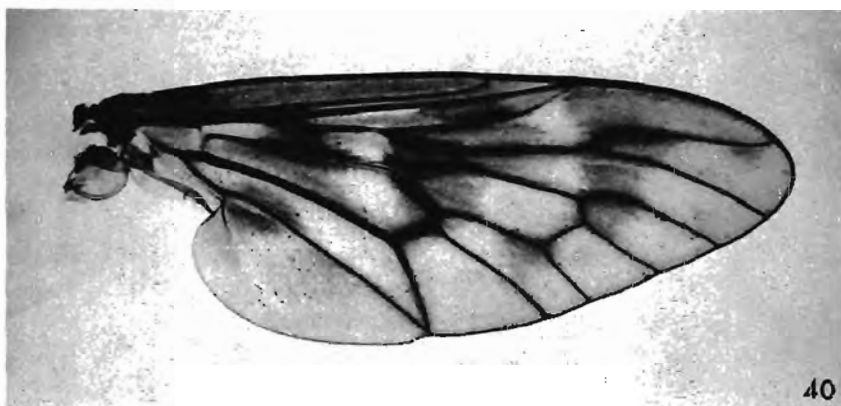
(c) Vein R_4 usually ends before the tip of the wing (as in Tabanidae); there are isolated exceptions to this, as in the genus *Atrichops*. In the rhagioniform genera R_4 often ends at the wing tip.

(d) The third posterior cell usually is widened apically; this is especially obvious in tropical species of *Suragina* (figs 44, 45), and is due to vein M_3 inclining towards M_4 . Sometimes the fourth posterior cell is closed by the apical fusion of M_3 and M_4 (as in *Xeritha*, some neotropical *Suragina* species, and some Tabanidae, e.g. *Aegophagamyia*). In the rhagioniform genera veins M_3 and M_4 are less convergent towards the wing margin, and they are often sub-parallel.

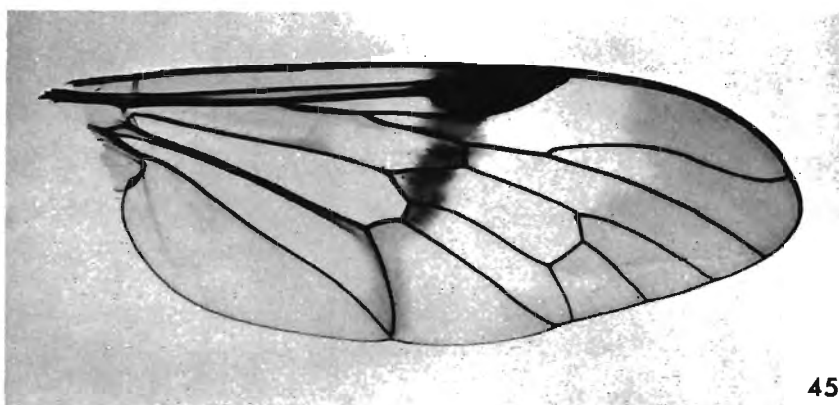
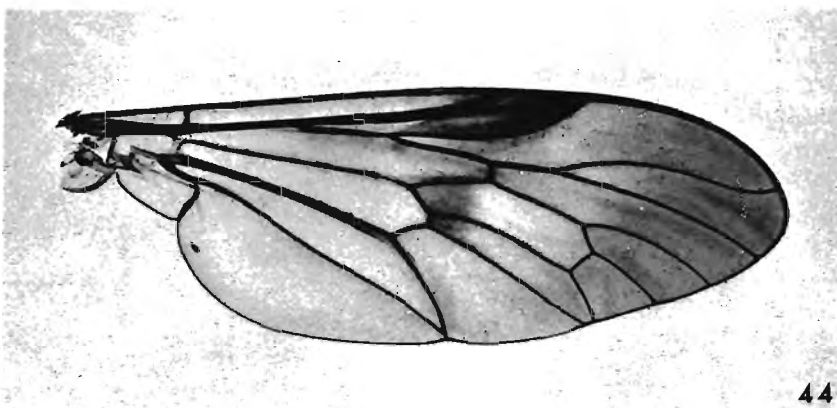
(e) The basal cells tend to be relatively more elongate in athericiform genera. There is overlap in this character but a comparison of figs 45 and 46 will reveal this feature.

(f) Correlated with lengthening of the basal cells is a displacement of the discal cell nearer the margin and corresponding shortening of the second and third posterior cells.

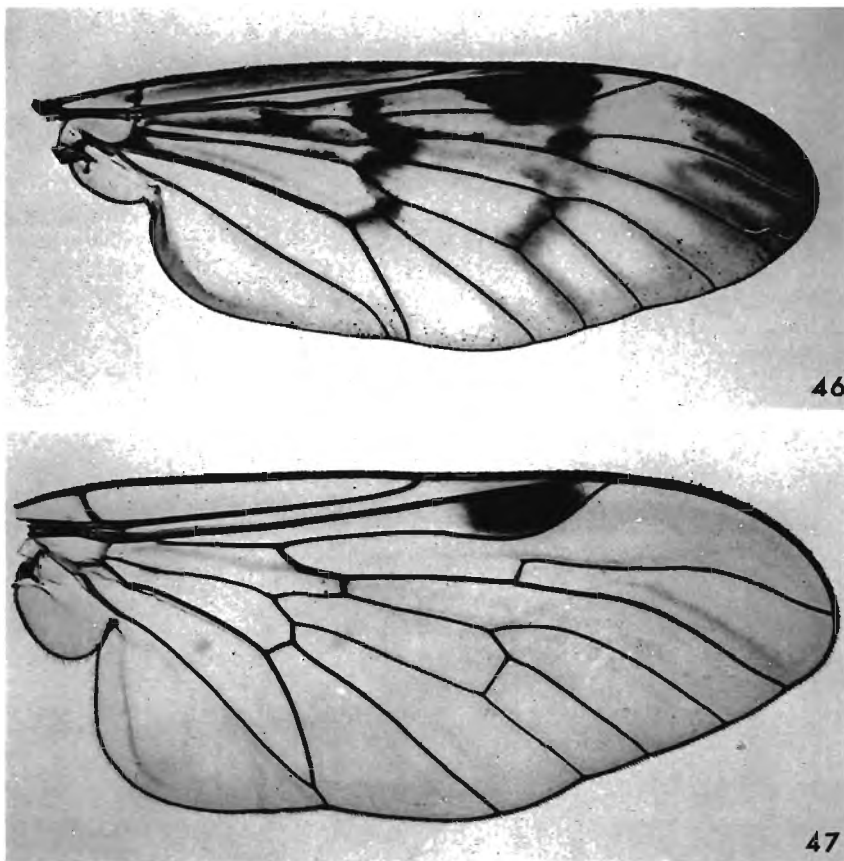
(g) The r-m crossvein meets the discal cell further from its basal end, and is often not opposite the basal section of M_4 at the apex of the second basal cell. Exceptions occur, but in general this is true. In the rhagioniform genera and Tabanidae, r-m is usually close to the base of the discal cell.



Figs 40-42. Wings (40) *Atherix ibis* Fabr.; (41) *Tabanus saxicolus* Usher; (42) *Rhagio tringaria* (Linn.).



Figs 43–45. Wings. (43) *Dasyomma* sp., Chile; (44) *Suragina monogramma* (Bezzi); (45) *Suragina milloti* (Séguy).



Figs 46-47. Wings. (46) *Rhagio scolopacea* (Linn.); (47) *Chrysopilus bisectus* Oldroyd.

(h) Vein M_1 is more gently arched than in the rhagioniform genera in which it is often strongly arched near the base.

6. The antennae

In nearly all the athericiform genera the third antennal segment is more or less reniform; *Dasyomma* is the only exception (*vide infra*). When reniform, its relative size is correlated with blood-sucking habits (it is larger in blood-suckers). In the rhagioniform genera the third segment is very variably shaped but reniform only in one genus, *Symphoromyia* (some species of which are blood-suckers). In Tabanidae the antennae are of a more plesiomorphic type in that a segmented style is consistently present.

DISCUSSION AND CONCLUSIONS

The morphological data presented above reveal clearly that the athericiform genera constitute a monophyletic group. The structural modifications of the abdomen and

specializations of the genitalia in both sexes, the presence of the postmetaspiracular 'scale', and the closure of the marginal cell, are apomorphous features; taken in conjunction, they are adequate evidence for grouping these genera in one suprageneric taxon. The monophyly of the group is also convincingly demonstrated by the morphology of the larval stages which are aquatic in all known cases (aquatic larvae are not known in the rhagioniform genera). Larvae of *Atherix* species are familiar and often illustrated, and closely resemble the larvae of *Suragina* and *Atrichops* (Nagatomi, 1961). I have larvae which circumstantial evidence indicates belong to *Trichacantha*, *Pachybates* and *Dasyomma* (the lastnamed from both Chile and Australia), and all conform to the *Atherix* type; they will be described in a subsequent publication.

The morphological data furthermore indicate that the sister-group of the athericiform taxon is not the rhagioniform genera but is the Tabanidae. The male and female genitalia provide excellent apomorphous characters demonstrating this: the endophallic tines and general structure of the aedeagus, elongation of the aedeagal apodemes, fusion of the male proctiger with the epandrium, and general pattern of reduction of segments in the female postabdomen. The presence in both groups of the postmetaspiracular 'scale' also indicates the relationship. And the nature of the postmetacoxal connection in the athericiform genera foreshadows the postmetacoxal bridge in Tabanidae and is an intermediate grade of evolutionary development. No other group in the lower Brachycera is synapomorphous in respect of the morphological features discussed above. The monophyly of the rhagioniform genera and their kinship with the Coenomyiidae is demonstrated by the apomorphous development of two-segmented female cerci.

Larval studies provide further important evidence for a close relationship between the athericiform genera and the Tabanidae. This matter is to be part of the content of a study on the larvae of the lower brachycerous groups being prepared by Dr L. Lyneborg and Dr H. Anthon of Copenhagen (*in litt.*), so I shall present no detailed discussion here. However, I wish to draw attention to the important paper by Schremmer (1951: especially pages 344-352 and 394) who demonstrates that *Tabanus* and *Atherix* have in common, as well as other similarities in larval head structure, a striking specialization in that the larval mandible ('die Gifthakenmandibel') contains a duct which conveys a poison from special glands to an apical orifice, the form of the mandible and nature of the glands being the same in both genera. In *Rhagio* the distal portion of the mandible has an internal channel but this does not open to the exterior apically, and there are no poison glands (Roberts, 1969: 385).

There seems no doubt that the Tabanidae are a monophyletic group, definable on the collective basis of apomorphous features of the wings, thoracic structure, postmetacoxal bridge, divided first tergite, united first and second sternites, male and female genitalia, and larval morphology. The athericiform genera are more plesiomorphic as regards wing venation, small squamae, more simple postmetacoxal connection, exposed female eighth tergite, and less compact body form; but more apomorphous in regard to antennal structure and possibly hypopygial structure. As this group of genera has a sister-group relationship with all Tabanidae, it must be consigned to a separate family, and this I formally propose now, viz. **Athericidae fam. nov.**, type-genus *Atherix* Meigen.

Selection of the type-genus, and hence the name of the family, has been problematical.

Atherix was selected because it is probably the most familiar genus, but in some features it is not representative (notably specializations of the aedeagus, female genital furca and first sternite, and the weakness of the postmetacoxal connection). There is also the unresolved problem of its type-species which is *Leptis ibis* Fabricius only by general consent; Verrall's (1909:284–286) argument on this matter is unacceptable, and James (1965: 344) is correct in stating that a decision by the ICZN is needed. *Suragina* Walker (1859) would appear to be a better choice because there is no problem about its type-species, it is by far the largest genus, and it occurs in all zoogeographic regions. However, future study may show that *Suragina* will have to be replaced by the earlier name *Ibisia* Rondani (1856). The type-species of Rondani's genus, *Bibio marginata* Fabricius, was considered by Verrall (op. cit.) and subsequent authors except Szilády (1934) to be a species of *Atherix*, but in my opinion that is incorrect because *marginata* does not have the specializations referred to earlier in this paragraph.

The best suite of characters to use for distinguishing the Athericidae from other lower brachycerous families is the following: marginal cell closed; postmetaspiracular 'scale' present; third antennal segment reniform (if not reniform, then other characters present, tibial spurs 1.2.2—genus *Dasyomma*); first tergite often divided in midline (especially in females), if undivided then the other characters unquestionably present. In addition, rhagionids have series of small, suberect bristles on the tibiae: these are absent in athericids. The elongate, telescoped postabdomen of the female is usually obvious in rhagionids, and often the two-segmented cerci protrude and can easily be seen in museum specimens. A careful study of the lower end of the metapleural epimeron will nearly always reveal the postmetacoxal connection in athericids, and in all athericid genera except *Dasyomma* there is a distinct suprametacoxal pit (*vide infra*).

Similarities indicating a close affinity between tabanids and athericids are found in biological features as well. In both groups the eggs are laid in clusters containing one or more layers; this has often been illustrated for Tabanidae, e.g. Schwardt (1936), Hine (1906), Marchand (1917), and Nagatomi & Tanaka (1968), and for Athericidae in the excellent paper by Nagatomi (1962). These clusters are cemented to an elevated substrate overhanging the larval habitat. Some athericids practise mass oviposition at favoured sites; this occurs in the South African genera *Trichacantha* (Stuckenberg, 1960) and *Pachybates* (Bequaert, 1921), and is well-known in *Atherix* (e.g. *ibis* in Europe and *variegata* in North America). Usually each female dies next to the egg-cluster she has deposited, a habit also found in some tabanids (Schwardt, 1936).

Most female tabanids are haematophagous, requiring a blood-meal for vitellogenesis. Exceptions are few and apparently involve groups whose larvae have invaded unusual habitats. In Athericidae haematophagous habits are known in the genera *Suragina*, *Atrichops* and *Dasyomma* (summary by Nagatomi, 1962: 106–112) and may also occur in the other genera with mandibulate females. The habit is relatively rare in Rhagionidae, being known only in some species of *Symphoromyia* and the Australian species of *Spaniopsis*. All athericids, but more noticeably the haematophagous species, share a habit with tabanids of appearing to stroke or palpitae the substrate ahead of the fly with the fore-legs; the fore-tarsi are slender and elongate in many athericids, and in both families are provided with long 'touch' hairs ventrally. Similar behaviour involving the use of the fore-legs is known

in some other lower brachycerous groups (see the translation by Verrall, 1909: 236, of a paper on this by Mik).

The internal classification of the Athericidae will be dealt with in another study. However, at this stage a major subdivision of the family can be made. Within the Athericidae there is only one AS group in Hennig's (1960) terminology, i.e. a monophyletic group distributed in both temperate South America and Australasia, and that is the genus *Dasyomma*. No other athericid genus has that type of distribution. Moreover, *Dasyomma* is also distinct in several morphological features:

(a) In all other athericids there is a suboval pit at the lower end of the metapleural episternum, above the upper corner of the metacoxa (figs 36, 38) (this pit is secondarily reduced in the morphologically bizarre South African genera *Pachybates* and *Trichacantha*). In *Dasyomma* there is no trace of a pit at that site.

(b) The tibial spur formula in *Dasyomma* is consistently 1.2.2; spurs on the fore-tibiae are exceptional in other genera of athericids, though they do occur.

(c) In *Dasyomma* the eyes have an abundance of long hairs except in a few unusual neotropical and Australian species; a number of other athericids have hairy eyes, but the hairs are always small and inconspicuous.

(d) In *Dasyomma* the third antennal segment is not reniform with a nearly dorsal arista as in the other genera, but subelliptical with an apical or almost apical arista.

(e) The palps in *Dasyomma* are decidedly elongate over the apical segment, almost cylindrical and clothed with long hairs, and sometimes slightly flexed apicad of the mid length; in other athericids the palps are relatively smaller, the apical segment is usually bent near the middle so that it is boomerang-shaped, and long hairs usually occur only in non-mandibulate species.

These seem to be adequate grounds for the segregation of *Dasyomma* taxonomically. The genus appears to have a sister-group relationship with all the other athericids, so a separate subfamily is required. I here formally propose the subfamily **Dasyomminae subfam. nov.**, monotypic for *Dasyomma* Macquart.

Finally, the division of the old family Rhagionidae made above requires a reconstitution of the Tabanoidea within the context of superfamilies composed by Hennig (*vide supra*). In brief, the Rhagionidae should now be transferred to the Xylophagoidea and placed adjacent to, or merged with, the Coenomyiidae; and also the Pelecorhynchidae should be transferred to that superfamily as they have an obvious kinship with, if indeed they are distinct from, the coenomyiids. Only the Tabanidae and Athericidae remain in the Tabanoidea.

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